SOME BIOLOGICAL CONSIDERATIONS OF FOREST PRODUCTION

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In some regions of the world, the forest is still regarded as a wild crop requiring little management apart from the felling and extraction of selected trees. The area of natural forest is gradually diminishing and most of the remaining unmanaged forests are not readily accessible for exploitation by man. Because of the continued reduction in the natural resources of timber in the world, intensive forest management to procure high productivity can be justified economically in Western Europe, where the demand for wood has far outstripped the supply. Within the last twenty-five years many new forests have been planted in Britain and these usually bear little resemblance to the natural forest cover, frequently consisting of even-aged monoculture stands of introduced tree species. Since agricultural production must be maintained on the better soil types, the new forests are located mainly in relatively infertile upland regions.

The successful establishment of these artificial plantations reflects the increasing domestication of British woodlands with the application of new sylvicultural techniques. Forest research workers have developed effective methods of site improvement such as deep draining, ploughing, manuring and sand fixation, so that sites which at one time would have been regarded as completely unsuitable for trees can now be afforested. More recently, increased attention has been paid to pruning and thinning procedures, since many of the new plantations are at the close canopy stage. Seed is available for planting from a wide range of tree species, both native and exotic, and tree-breeding is being practised on quite a large scale in order to ensure a supply of trees having desirable qualities. In reality, sylviculturalists are attempting to domesticate trees just as herbaceous plants were domesticated for agriculture, but the process is inevitably much slower with trees since the forest crop may take over a hundred years to mature. With the application of such intensive forest research, the general productivity of British woodlands will increase, but can this increase be maintained indefinitely for successive tree crops, and is there any natural maximum limit to the annual productivity? Surprisingly little is known about the basic ecological factors that control the biological productivity of woodlands when several timber crops are harvested over long periods of time.

Comparisons of the growth of different tree species grown under comparable site conditions have been made by sylviculturalists in many experimental areas in Britain. Frequently, great variations in growth have been recorded not only between plantations of different species but also between plantations of the same species raised from seed collected from different localities. Largely as a result of this research, it is now possible to make a broad classification of sites into different productivity-ratings, and to forecast the growth of certain tree species or varieties, at least on a short term basis. The precise relationships between the productivity of British woodlands and soil factors such as structure, nutrient status and drainage, are not yet clear. In America, tree growth has been closely correlated with the physical condition of the soil (Coile 1952).

However, it is not easy to measure accurately the productivity of woodlands, largely because of the great size and age that trees may attain. In addition, the forest crop differs from most agricultural crops in that it is harvested over a long period of time during which the annual production may vary considerably. The productivity of a forest plantation is normally assessed from measurements of bole height and girth, which are converted to marketable wood volume. Consequently, there is little information on the productivity of British woodlands on the basis of dry weight, or on the total dry matter production of trees, inclusive of the canopy and roots.

The great differences in the volume production of plantations in species trials obviously reflect differences in the dry weight of the plantations, and at several experimental areas in Britain estimates of this have been made (Ovington 1956). In general, greater amounts of dry matter are produced by evergreen coniferous species than by the deciduous hardwoods. For instance, at Bedgebury where the trees are twenty-one years old, a plantation of Norway spruce (*Picea abies*) has produced 164,000 kilograms of bole material per hectare compared with 34,000 kilograms for oak (*Quercus robur*). Similarly at Abbotswood, which was planted forty-seven years ago, the weights of bole produced by Norway spruce and oak are 394,000 and 126,000 kilograms per hectare respectively. The stem-wood, which is the main economic product of British woodlands, represents only part of the total dry matter produced by the trees. In the plantations of spruce at Abbotswood, for instance, the canopies (branches and leaves) of the standing trees are about half the weight of the boles.

In order to investigate the productivity of single trees and plantations over one rotation, I have made growth studies in an age series of plantations of Scots pine (*Pinus sylvestris*) at Thetford Chase (Ovington 1957). The weight of a standing tree does not represent the total weight of dry matter produced by the tree during its lifetime, since some of the outer bark, leaves, cones, branches and roots die annually. The loss of dry matter by mortality varies considerably for the different parts of the tree but, in general, the greatest loss is for leaf material, since leaves are relatively short lived. The total dry weight of a fifty-five year old pine at Thetford Chase is about 200 kilograms (Table 1), but in the course of its life over 300 kilograms of dry matter will have been produced.

TABLE 1

The dry weight in kilograms of average trees of *Pinus sylvestris* grown in plantations at Thetford Chase.

Age yrs.	*Cones*	*Living branches*	*Dead branches*	*Leaves*	*Bole*	*Roots*	*Total living parts*
7	0	0.20	0	0.04	0.21	0.70	1.15
11	0	1.02	0.01	1.37	1.24	2.51	6.14
14	0.01	1.50	0.27	1.29	1.62	2.00	6.42
17	0.13	1.67	0.45	1.59	2.88	2.26	8.53
20	0.32	2.22	1.21	1.94	5.02	2.60	12.10
23	0.11	3.80	3.58	1.39	12.18	7.71	25.19
31	0.09	3.97	5.67	3.49	34.45	11.67	53.67
35	0.38	5.08	8.07	5.20	52.28	23.49	86.43
55	0.63	16.12	13.20	9.52	127.21	44.84	198.32

The dry weight of all the trees comprising a plantation can be estimated by multiplying the average tree weight by the stocking density (Table 2). This does not give the total production by the trees since, apart from losses through mortality, trees are being removed continually as the crop is harvested. The weight of timber extracted increases rapidly about twenty years after planting, and for the pine plantations at Thetford Chase the average weight of trees felled per annum in an hectare of woodland is equivalent to about 8,000 kilograms of dry matter. Approximately half of this is bole, so that only about 4,000 kilograms of dry matter would be removed from the woodlands.

TABLE 2

Dry matter production by plantations of *Pinus sylvestris* at Thetford Chase.

Age in years	7	11	14	17	20	23	31	35	55
Dry wt. of trees 1,000 Kg./Ha.	7.5	26.0	33.3	48.1	65.4	91.7	127.2	163.4	150.7
Wt. dry matter produced 1,000 Kg./Ha.	8.1	30.9	50.0	85.4	118.9	217.7	348.4	445.2	682.9

It is interesting that, although the weight of leaf on individual trees increases with age, the weight of leaf carried on the plantations does not increase indefinitely but tends to reach a fairly constant weight about twenty years after planting. The maximum dry weight of leaf recorded in the Scots pine plantation was 10,000 kilograms per hectare with a leaf area of nearly eleven hectares, but the maximum value is different for other tree species and depends also on the location. Burger (1941) found that a forty year old spruce woodland had 44,000 kilograms of leaf (fresh weight) per hectare, giving a surface area of twenty-eight hectares. The constancy of leaf weight in dense forests of the same species but of different ages seems to indicate that some kind of equilibrium has been reached between the trees and the existing ecological conditions of light, climate and soil.

The annual increment of dry matter varies considerably, depending upon the age and stage of development of the plantation. Initially, there is little competition for light or soil space between the individual trees of a plantation, and the annual production per unit area is relatively small. After the individual tree canopies have met to form a dense cover over the ground and the root systems have become ramified throughout the available soil volume, the productivity of the woodland reaches a maximum value. Later, annual productivity declines as the tree stand reaches maturity and is heavily cropped. The maximum current annual increments of dry matter attained at about twenty-five years of age are approximately 1,000, 3,000, 4,000, 5,000 and 9,000 kilograms per hectare for cones, roots, leaves, branches and boles respectively. A plantation of Scots pine grown on the sandy Thetford soils will produce about 700,000 kilograms of dry matter per hectare within fifty-five years, irrespective of any losses caused by respiration. Möller, Müller and Nielson (1954) have found that the loss of dry matter by respiration in stem and branches is about five per cent of the dry matter of beech (*Fagus sylvatica*).

The efficiency of the pine plantations at Thetford Chase in utilizing the site factors for the production of dry matter can be evaluated by comparing them with local agricultural crops. On the average, agricultural crops grown nearby produce about 5,000 kilograms of dry matter per hectare annually, and the maximum value recorded for an agricultural crop was about 9,000. A high level of production by agricultural crops is maintained by a considerable expenditure on cultivation and manuring, but the Scots pine plantations have not been ploughed or manured. The comparatively high annual yields which they attain during the period of productivity seem to be associated with the huge mass of leaf and root accumulated by the trees. Most agricultural crops are planted each year as seed and develop complete leaf and root systems annually, while dense stands of pine may have over 10,000 kilograms of leaves and 40,000 kilograms of roots throughout the whole year, so that they are able to utilize the site at all times. There is evidence that evergreen tree species photosynthesize whenever weather conditions are suitable, even during the winter period (Parker 1953).

The annual increment of dry matter for plantations of different trees varies considerably, and on many sites other species are capable of greater annual increments than *Pinus sylvestris*. At Abbotswood, for instance, the average annual increments recorded for *Pseudotsuga taxifolia* and *Pinus nigra* are much greater than that for Scots pine. These differences in productivity can be related to some extent to differences in site utilization as expressed through the total weights of leaves and roots developed. It is clear that forests, compared with other vegetation types, are able to absorb and store a considerable proportion of the incident solar energy and are efficient producers of organic matter.

Trees differ greatly in their chemical composition, not only from species to species but also when trees of the same species are grown under different conditions. The quality as well as the quantity of the dry matter must be considered in comparing the productivities of different woodlands. The differences in chemical composition between *Quercus robur* and *Picea abies* grown in adjacent and similar plots are shown in Table 3.

TABLE 3

The average chemical composition of *Quercus robur* and *Picea abies* at Abbotswood.

	Ash	*C*	*N*	*Na*	*K*	*Ca*	*Mg*	*P*
	(as percentages of O.D. wgt.)				(as mg./100 g. O.D. wgt.)			
Quercus robur								
Leaves	5.63	56.15	2.91	20	1,200	1,030	220	250
Canopy	1.12	55.08	1.01	6	485	336	82	95
Bole	0.64	59.25	0.14	2	111	162	22	11
Picea abies								
Leaves	4.38	60.58	1.53	60	500	660	90	120
Canopy	2.31	59.18	0.71	11	207	385	62	80
Bole	0.41	63.41	0.07	2	33	109	19	10

Although trees are not so rich in plant nutrients as herbaceous plants, the total amounts contained within a tree crop may be large because of the huge size to which trees can grow (Table 4). At Abbotswood for instance, the trees may contain up to 800 Kg. of nitrogen, 15 Kg. of sodium, 400 Kg. of potassium and 80 Kg. of phosphorus per hectare of plantation. Because of the large uptake of nutrients from the soil by forest crops and the low nutrient content of some of the soils available for afforestation, there is an apparent danger of soil impoverishment under continued economic management. It would appear to be difficult to maintain indefinitely the productivity of woodlands on a sustained yield basis, without some artificial means of soil improvement to counteract the removal of nutrients from the soil by trees. Once trees are established the nutrient uptake and turnover of the ecosystem are changed, and the direction and rate of soil change depends both upon the initial soil conditions and the species used for afforestation (Ovington and

Madgwick 1957). The depletion of soil nutrients or their redistribution within the soil profile could result in decreasing productivity for successive forest crops. However, the nutrient relationships existing between woodland plants and soils is extremely complex, and it would be unwise to make generalization from crop analysis alone. Considerable fundamental research is needed before the dangers of lowered productivity as a result of long term soil impoverishment can be fully appreciated. Relatively little is known, for instance, of the rate of release of mineral elements by the breakdown of soil particles and the loss of nutrients by leaching under woodland conditions.

TABLE 4

The total weights of chemicals contained in forty-seven year old stands of *Quercus robur* and *Picea abies* at Abbotswood.

	C	*N*	*Na*	*K*	*Ca*	*Mg*	*P*
	1,000 Kg./Ha.			Kg./Ha.			
Quercus robur							
Canopy... ...	12.0	218	1.4	105	73	18	21
Boles	63.1	151	2.5	118	173	23	11
Picea abies							
Canopy... ...	47.5	573	9.0	166	309	50	64
Boles	115.7	132	2.9	60	198	35	18

Mixed plantations, including species to enrich the soil, have been advocated as a means of ensuring soil conservation and forest production. From the long term point of view, the productivity of commercial woodlands may have to be considered in relation to the application of fertilizers to maintain the nutrient content of the soil. The main importance of mixed plantations in maintaining productivity may prove to be the reduction of the rate of spread of the catastrophic diseases to which monoculture stands are particularly subject.

The biological productivity of a woodland cannot be assessed solely in terms of the dry matter produced by the trees. At certain stages in the history of a woodland the ground vegetation, for instance, may become very luxuriant. In dense forests either there is no ground flora or it is poorly developed, but as the trees are progressively thinned and the canopy is opened up, it becomes more abundant. In the age series of plots of *Pinus sylvestris* at Thetford Chase, it has been possible to examine the gradual development of the ground flora from 100 kilograms per hectare at twenty years of age to 2,700 kilograms at fifty-five years. In the older plantation the total weight of leaves on the trees is three times as much as that of the ground flora, which almost equals that of the annual leaf-fall. When the associated vegetation has become as luxuriant as this, the trees cease to be the dominant feature in the productivity of the ecosystem, and cannot be regarded as making full use of the site. From the viewpoint of obtaining the maximum productivity of trees, it would be advantageous to underplant or encourage natural regeneration before this stage is reached, so that when the old trees are removed the young seedlings will be well developed and will rapidly form a close canopy.

The type of ground flora found in woodlands is determined to some extent by the tree species that are present and the forest management that is applied. A luxuriant vegetation dominated by bracken develops under pine at Abbotswood, whilst in adjacent stands of oak, grasses such as *Holcus mollis* and herbaceous plants such as bluebell (*Endymion nonscriptus*) and wood sorrel (*Oxalis acetosella*) are more abundant. The herb layers formed in different tree stands differ greatly in their chemical composition, just as the trees differ, and the mineral composition of the woodland vegetation is usually relatively high. Although grazing is permitted in some of the older Royal forests such as the Forest of Dean and the New Forest, little attention has been paid in Britain to the possibilities of controlled grazing in commercial woodlands. If grazing by either domestic or wild animals could be permitted at certain stages of forest development, it might form a useful means of converting the high carbohydrate productivity of woodlands to protein. This multipurpose use of land could be further developed by having the same area of land used alternately for forestry and grazing.

Woodlands are complex ecosystems, the productivity of which is extremely difficult to determine. Whilst sylvicultural research is likely to develop techniques to improve the annual increment, there is evidence that woodland productivity is already being limited by basic site factors. If timber production is to be maintained indefinitely, the long-term effects of woodlands on the site must be carefully considered. However, with our present knowledge, it is possible, even on sites with soils of low nutrient status, to obtain very high productivities as measured by the formation of organic matter. Only a small proportion of the dry matter produced by a woodland cover is harvested by man and there is considerable scope for increasing the utilization of forest production.

REFERENCES

BURGER, H. 1941. Holz, Blattmenge und Zuwachs. 5. Mitteilung. Fichten und Föhren verschiedener Her Kunft auf verschiedenen Kulturorten. Mitt. d Schweiz. *Anst. f. d. forstl. Versuchsw.*, **22**, 10–62.

COILE, T. S. 1952. Soil and the growth of forests. *Adv. in Agron.*, **4**, 329–98.

MÖLLER, C. M., MÜLLER, D. & NIELSEN, J. 1954. Respiration in stem and branches of beech. *Det Forstlige Forsφgsvaesen i Danmark*, **3**. 273–301.

OVINGTON, J. D. 1956. The form, weights and productivity of tree species grown in close stands. *New Phytol.*, **55**, 289–304.

OVINGTON, J. D. 1957. Dry matter production by *Pinus sylvestris* L. *Ann. Bot. N. S.*, **21**, 287–314.

OVINGTON, J. D. & MADGWICK, H. A. I. 1957. Afforestation and soil reaction. *Jour. Soil Sci.*, **8**, 141–9.

PARKER, J. 1953. Photosynthesis of *Picea excelsa* in winter. *Ecol.*, **34**, 605–9.

DISCUSSION

O. V. S. Heath. In view of the apparent importance of the ground vegetation in forestry may I ask if any experimental attempts have been made to grow some leguminous under-crop, at least during the earlier stages before shading by the trees becomes too severe?

J. D. Ovington. In the experimental forest plots of the Forestry Commission on the North Yorkshire Moors, broom (*Sarothamnus scoparius*) has been planted in mixture with spruce and has improved its growth. At Yarner Wood Nature Reserve, the Nature Conservancy have planted broom in a series of experimental plots to see if it will improve the growth of oak. Alder has also been used as a nurse species by the Nature Conservancy and probably acts in a similar manner to leguminous plants in increasing the nitrogen content of the soil.